STEM MORPHOLOGY OF THE RECENT CRINOID
CHLADOCRINUS (NEOCRINUS) DECORUS

by S. K. DONOVAN

ABSTRACT. The modern crinoid *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson) has a column which is divided into a short proximal growing region, and a longer distal portion in which the arrangement of columnals remains constant. Lumen shape is pentagonal just beneath the cup but is circular for most of the length of the stem. Articular facet morphology shows considerable variation proximally but is constant in the dististele except between nodals and infranodals, where articulation is synostosial rather than symplexial. Cirri are quite different from the column, being elliptical with elliptical lumina and synarthrial articulation between cirral ossicles. Lumen shape is more constant than columnal outline or facet morphology, so it is concluded that the Russian system of naming morphogenera, which emphasizes lumen shape, is preferable to that of Moore (1939*a*), which stresses columnal outline.

IT is possible to describe crinoid columnals and to group those of a similar morphology together, but the reconstruction of complete crinoid stems from dissociated ossicles is generally impracticable. New vertebrate taxa can often be described from minimal evidence (e.g. Rieppel 1982) because the number of bones in the skeleton and their arrangement remains reasonably constant throughout the group, despite the great variation in vertebrate morphology. Crinoid columns, however, differ from the vertebrate skeleton by showing great variation in the number, shape, and arrangement of units (i.e. columnals, which are broadly analagous to bones), even within members of the same genus (compare, for example, the columnals of *Colpodecrinus quadrifidus* Sprinkle and Kolata, 1982 and *C. forbesi* Donovan, 1983*a*). Dissociated columnals are not usually sufficiently distinct for them to be classified with confidence, and can usually only be named by inclusion within artificial morphogenera (Moore 1939*a*; Yeltysheva 1955, 1956).

Few detailed studies have been made of the variation shown within a crinoid column, so there is only minimal reference material available. Jeffords and Miller (1968) examined four columnal taxa for which numerous good specimens were available. Growth stages were determined by examination of internodal insertion, the relationship between columnal diameter and the number of culmina (radiating ridges on the articulation surface), and the nature of longitudinal sections. Each of the columnal types showed a distinct sequence of development. Comparison of columnal diameter with the number of culmina was shown to be a useful method of ontogenetic analysis, although good preservation is necessary for this to be applied to fossil material. Roux graphically determined the relationship between columnal height and diameter in the Bourgueticrinina (1977*a*) and the Millericrinidae (1978). This is reasonable if good material is available, but Ordovician columnals, for example, are often preserved as external moulds. Unless a counterpart is available, it is not usually possible to determine the height of columnals preserved in this manner.

A number of parameters were used in bivariate analyses of Devonian columnal morphospecies by Le Menn (1981); of these, graphs of articular facet diameter against columnal diameter, lumen diameter against articular facet diameter, and columnal height against columnal diameter are of the greatest general utility. Plots of columnal diameter against lumen diameter and against columnal height have proved most useful in the analysis of Ordovician columnals (Donovan 1983*b*, pp. 68–74).

The problem remains, however, that little detailed information is available concerning the morphology of columns in individual crinoids. In this paper the stem of the recent isocrinid *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson, 1864) (Breimer 1978, p. T9, footnote; Rasmussen 1978, p. T857) is considered. Reichensperger (1905) described the anatomy of this species

and determined the organization of soft tissues in the axial canal (see Jefferies 1968, p. 259, fig. 5, after Reichensperger). Roux (1977*b*), in his review of isocrinid stalk joints, described the articular facets of *C. decorus*. In the present study the whole stem of *C. decorus* is described; particularly the changes that occur between different parts of the column, so that comparison can be made when similar variations are detected in fossil columns. *C. decorus* is an articulate, and therefore in a different subclass to all Palaeozoic crinoids, but it is probable that the morphological variations which it shows are determined by stem function and that similar variations which occur in other pelmatozoans, regardless of age or systematic position, are also functional in origin.

A recent crinoid, rather than a fossil species, has been chosen for this study of gross stem morphology because of the ease with which the column can be disarticulated and sectioned, examined functionally (e.g. comparing the flexibility of the proxistele and dististele), and prepared for SEM study of the microstructure. Stem terminology follows Moore, Jeffords, and Miller (1968), Roux (1977*b*), Ubaghs (1978), and Webster (1974). Features of the articular facet of *C. decorus* are illustrated in text-fig. 3. Other terminology applied to the crinoid stem is explained in text-figs. 1, 5, and 6. Terminology of stereom microstructure follows Smith (1980). The stem is divided into two distinct skeletal systems: the column (composed of individual calcite plates called columnals) and associated cirri (jointed appendages, in this example adapted for attachment, composed of cirral ossicles).

MATERIALS AND METHODS

This study is based on two specimens exchanged with the Smithsonian Institution, Washington DC, USA. The exchange was initiated by Dr. David L. Pawson of the Department of Invertebrate Zoology at my request. Both specimens formed part of a group registered with the United States National Museum as USNM 12356 *Isocrinus decorus* and are referred to in the text as USNM 12356/1 and 12356/2. Labels attached to the specimens state '*Pentacrinus decorus* Wyv. Th. Off Havana, Cuba; Sta. 2,319–2,350. U.S. FISH COMMISSION, Steamer Albatross, 1885'. Both were damaged but the most complete specimen (USNM 12356/1) had an entire stem, broken into a number of pieces, which was disarticulated to obtain most of the ossicles shown in Plates 73–75. Ossicles from USNM 12356/2 are illustrated in Plates 73 and 76, and the 'whole' specimen in text-fig. 2. Both specimens are to be returned to the Smithsonian Institution.

Ossicles were disarticulated using Milton 2 sterilizing fluid diluted with an equal volume of water. The process was observed using a 'Wild' binocular microscope so that ossicles could be removed from the solution as they dissociated. This enabled ossicles to be selected for examination before complete disarticulation into a mass of plates. Columnals treated in this manner had all soft tissues dissolved. The ossicles were then washed and dried with a gentle heat source. Plates for examination under SEM were mounted on stubs using 'Durofix' glue or doubled-sided 'Sellotape.' Coating of stubs with 60% gold-palladium was carried out in the Department of Botany, University of Liverpool.
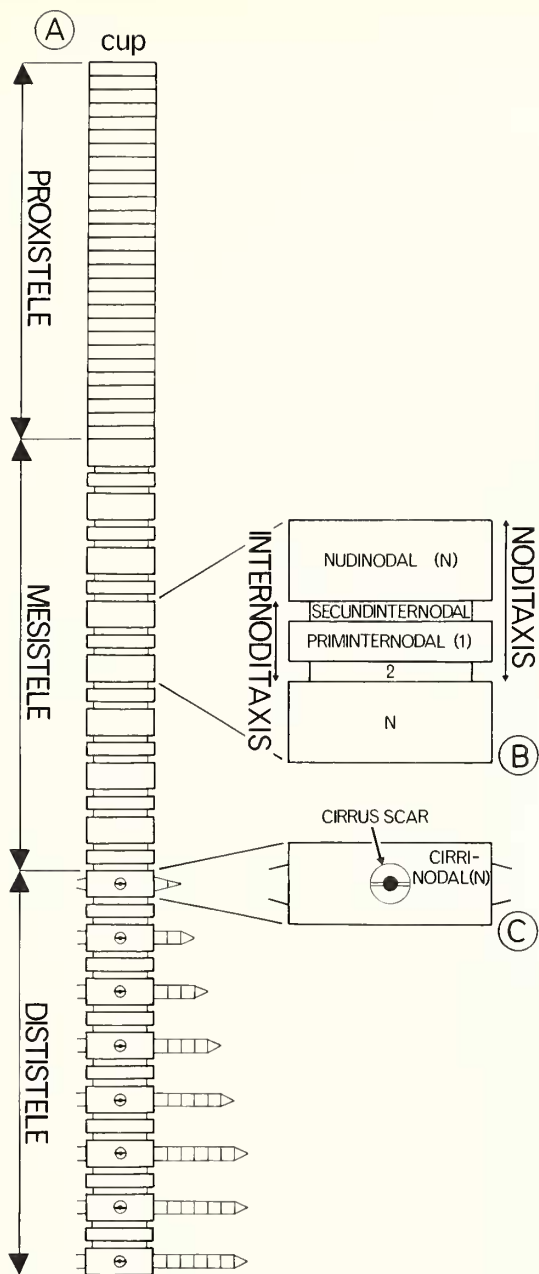
COLUMN AND COLUMNALS

The stem of *C. decorus* can be divided into two distinct regions, a proxistele (i.e. the stem proximal to the cup), and a relatively longer dististele (at least five times as long, although this is probably variable due to autotomy; Emson and Wilkie 1980) (text-fig. 1A). Stems such as this example, which can be divided into two or more morphologically distinct regions, are called xenomorphic. Using Webster's notation (1974; N = nodal, 1 = priminternodal, etc.; see text-fig. 5), and dividing the column into noditaxes (text-fig. 1B), the columnals which can be seen in the proximal region of USNM 12356/2, without sectioning, are:

(cup)–212N–212N (first cirrinodal)–212N–2123N–3231323N–3231434243N– 3424341434243N (25·0 mm below base of cup)–3424341434243N–3424341434243N (54·5 mm).

The proximal stem of USNM 12356/1 was (before disarticulation):

(cup)–?N–N–1N (first cirrinodal)–1N–1N–212N–212N–3231323N– 3231323N (11·5 mm)–3424341434243N (19·0 mm)–3424341434243N (25·5 mm).

A cup

PROXISTELE

MESISTELE

INTERNODITAXIS

NODITAXIS

NUDINODAL (N)

SECUNDINTERNODAL

PRIMINTERNODAL (1)

2

N

B

CIRRUS SCAR

CIRRI-
NODAL(N)

C

DISTISTELE

TEXT-FIG. 1 (*left*). A–C, hypothetical stem showing three morphologically distinct regions (only two are seen in *Chladocrinus* (*Neocrinus*) *decorus*), the proxistele, mesistele, and dististele. A, schematic diagram of the complete stem; cirri (attachment structures) only occur in the dististele of this example, unlike the stem of *C*. (*N.*) *decorus*. B, part of the mesistele (middle stem). *C*. (*N.*) *decorus* has a column which can be divided into two distinct regions only, and is not regarded as having a 'middle stem' unlike many other crinoids. The largest columnals are nudinodals (i.e. nodals that do not bear cirri). Priminternodals are larger than secundinternodals. A taxis is a sequence of ossicles. The internoditaxis includes all ossicles (internodals) between two sequential nodals. The noditaxis comprises a nodal with associated internoditaxis. C, cirrinodal of the dististele; cirri articulate on small facets, called cirrus scars, on the nodal latera.
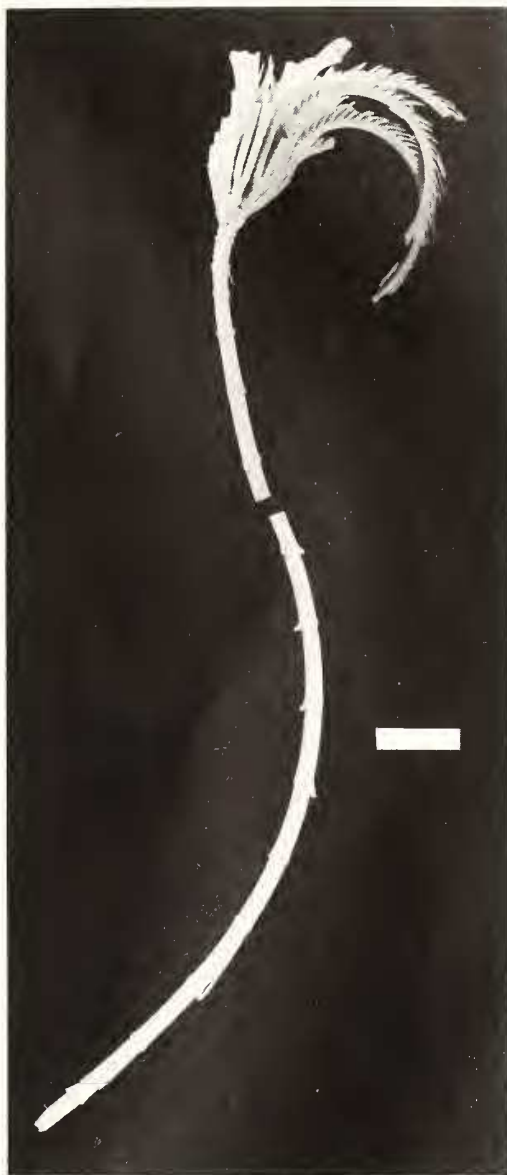
TEXT-FIG. 2 (*right*). *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson). USNM 12356/2. The most distal part of the column, many of the cirri, and some of the arms are missing. Scale bar represents 2cm.
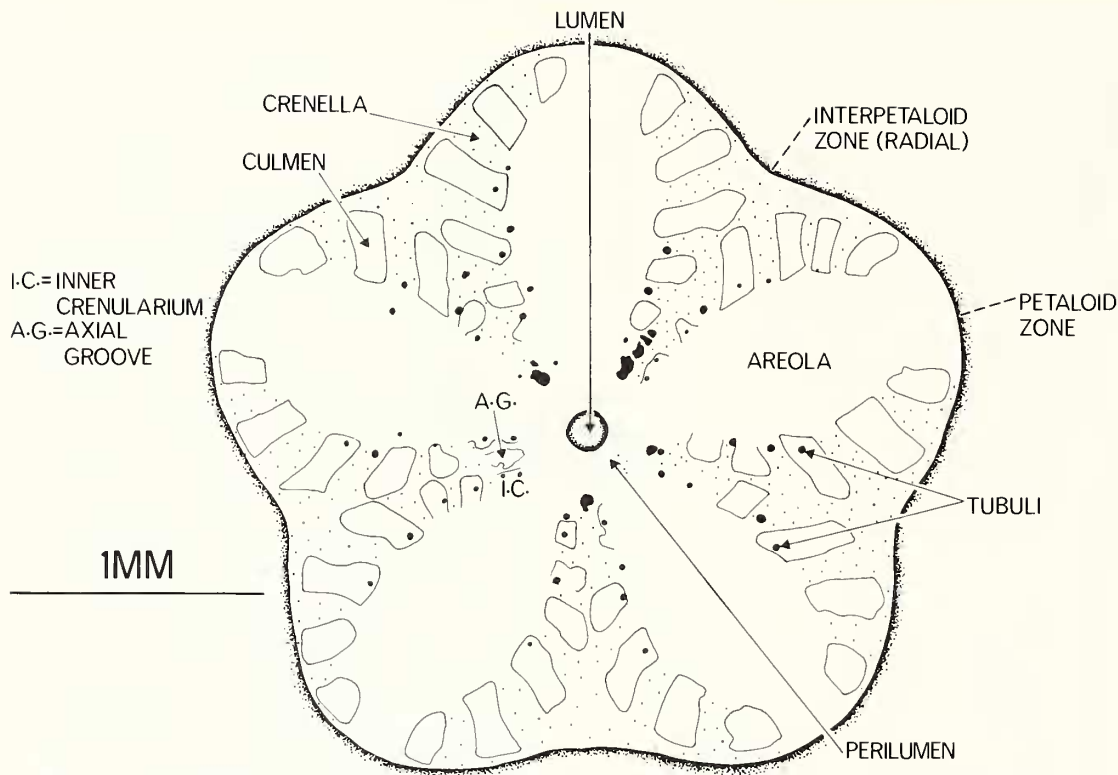
TEXT-FIG. 3. *Chladocrinus (Neocrinus) decorus.* USNM 12356/1. Proximal articular facet of a nodal (traced from an enlargement of Pl. 74, fig. 2).

The Webster chart for USNM 12356/2 represents the entire proxistele, whereas the chart for 12356/1 is slightly less. The variation which can occur in the arrangement of columnals in the proxistele is apparent when the two charts are compared. Breimer (1978, p. T23, fig. 10) illustrates the most proximal part of the column of another specimen of *C. decorus.*

The most proximal columnals apparent are very thin. Between these and the base of the cup occur a number of cryptic ossicles (for example, three between the cup and ?N of USNM 12356/1) which are very small, pentastellate in outline, a single stereom layer thick, and extremely delicate; these are presumably incipient nodals. Similarly, internodals of the same appearance are formed in the proxistele between more mature columnals, and are also hidden from view until they are as wide as the adjacent columnals. These cryptic columnals are accommodated during their early growth stages in concave regions of the proxistele, either at the base of the cup (Pl. 73, figs. 2, 8) or in the petaloid zone of concave columnals (Pl. 74, fig. 7; the petaloid zone is the principle area of ligamentation of

EXPLANATION OF PLATE 73

Figs. 1–8. *Chladocrinus (Neocrinus) decorus* (Wyville Thomson). USNM 12356/1 (figs. 1, 2, 6–8) and 12356/2 (figs. 3–5). Scanning electron micrographs of the stem and cup. 1, noditaxis N3424341434243; the upper nodal is the more proximal, × 12. 2, 7, 8, the base of the cup: 2, general view of the whole cup, × 6; 7, lumen at the base of the cup, × 80; 8, a single basal plate, × 25. 3, 5, cryptosymplexies of distal nodal facets, × 56 and × 120 respectively. 4, articular facet showing ligament fibres concentrated in petaloid zones, × 12. 6, poorly preserved proximal internodal (cf. text-fig. 4c), × 60.

PLATE 73

DONOVAN, *Chladocrinus* (*Neocrinus*)
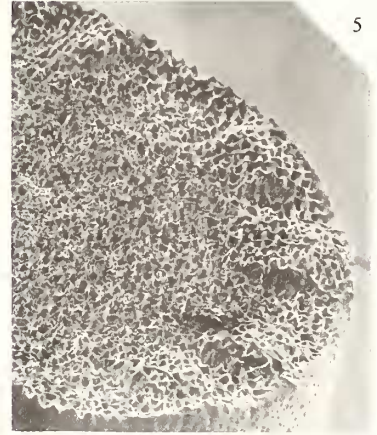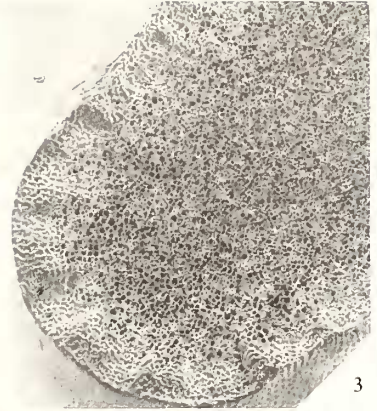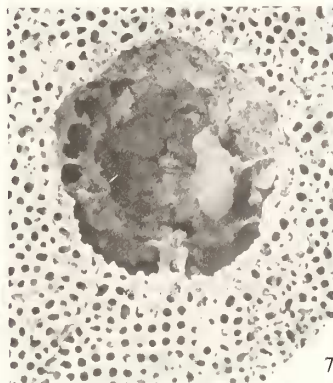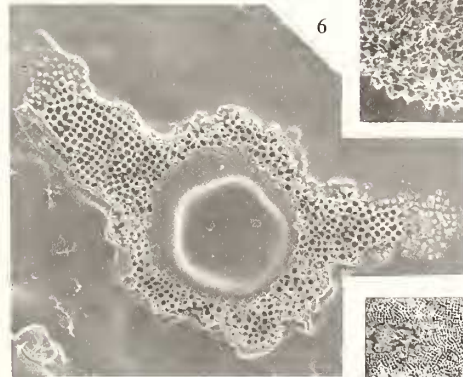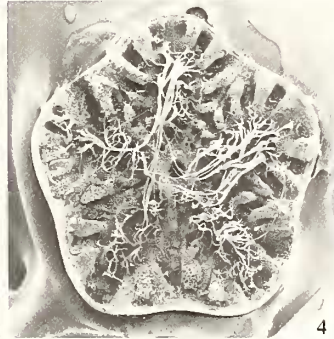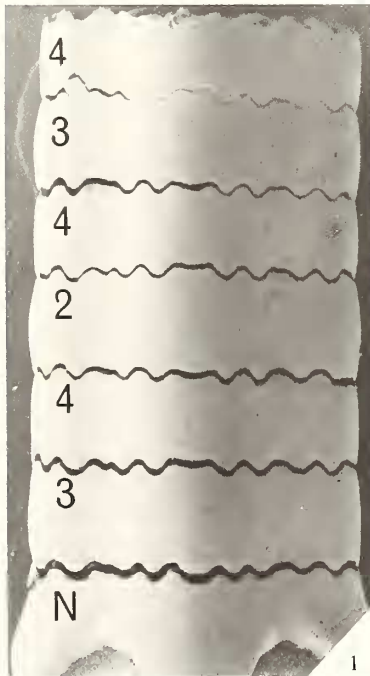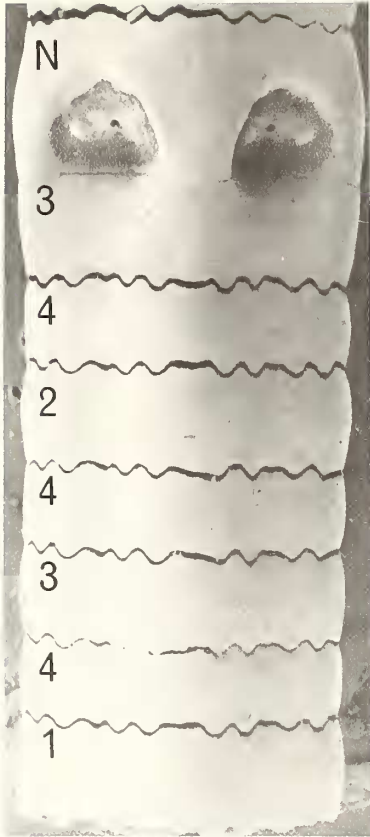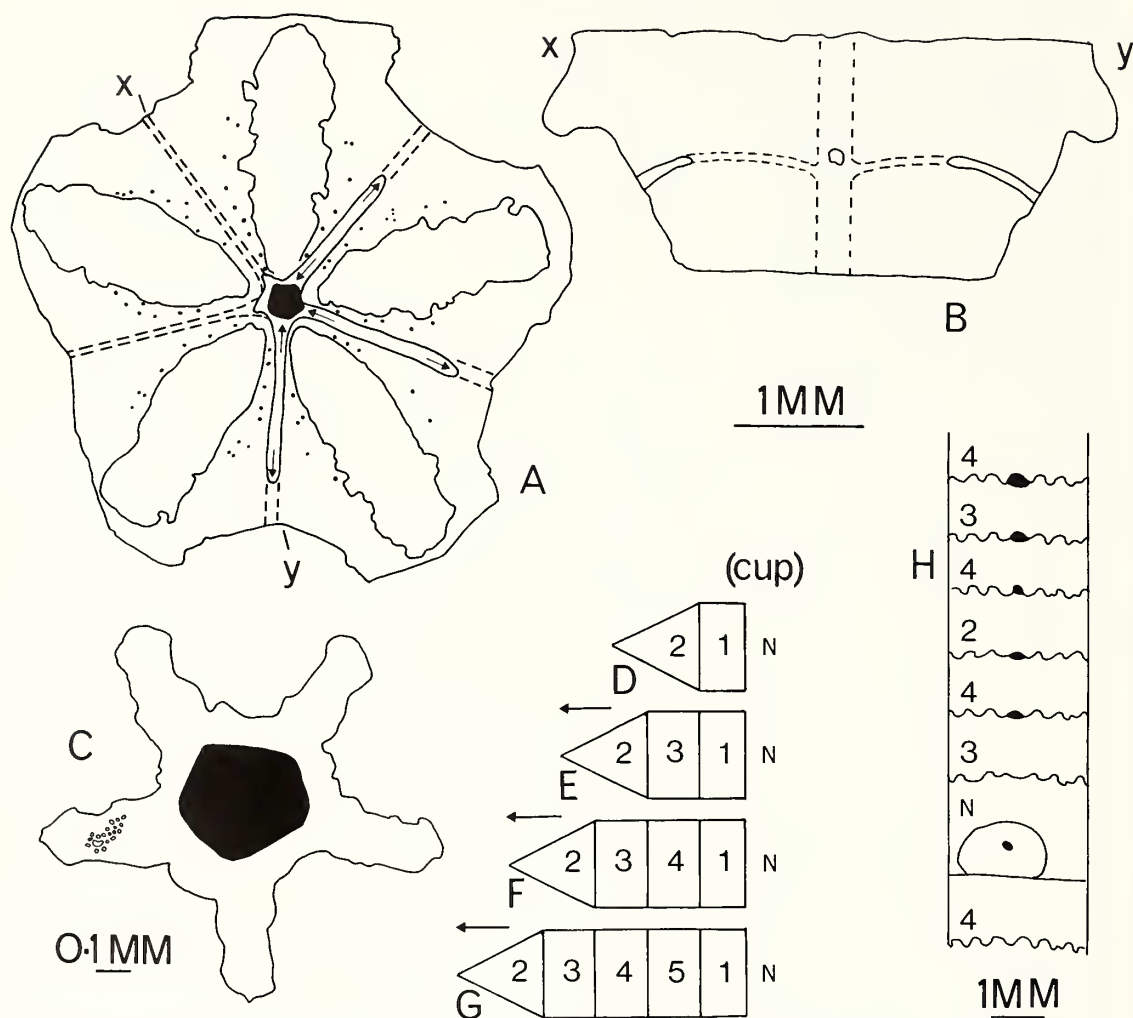
TEXT-FIG. 4. *Chladocrinus* (*Neocrinus*) *decorus*. A–C, USNM 12356/1. Transverse (A) and longitudinal (B) sections through nodals at the junction between the axial canal and cirral canals, i.e. canaliculi. A, three canaliculi cut by section, all five being completed as dashed lines. Arrows point down dip. Orientation of diagram looking distally, i.e. away from the cup. Tubuli shown as black dots and axial canal of the columnal shaded black. Irregular oval areas correspond to rectilinear stereom. B, longitudinal section x–y from A, showing the orientations of the axial canal and canaliculi (cup towards the top of the page). C, reconstruction of the facet of a proximal internodal (cf. Pl. 73, fig. 6); some stereom pores outlined (lower left). D–G, sequence of formation of new cirrals (numbers refer to order of formation, N = nodal). D, most proximal cirrus, formed of primary cirrals 1 and 2. E, cirral ossicle 3 intercalated between 1 and 2 on a slightly more distal nodal. F, cirral ossicle 4 appears between 1 and 3. G. cirral ossicle 5 is intercalated between 1 and 4. H, USNM 12356/2. Junction between the dististele (the first columnal of which is the lowest quartinternodal) and the proxistele; fossulae (between columnals) and canaliculi shaded black. A–C and H are camera lucida drawings. The longest scale bar refers to A and B.

a columnal facet). A damaged internodal in its early growth stages has been examined (Pl. 73, fig. 6) and a reconstruction of the columnal made (text-fig. 4c). A slightly more advanced columnal is also shown (Pl. 74, fig. 6). The crenularium (i.e. the alternating arrangement of ridges and grooves— culmina and crenellae, respectively—which interlock to provide a rigid suture between adjacent columnals) has yet to develop.

The proxistele is much more flexible than the dististele. This is because it is composed of thin columnals of variable height and diameter which are able to adjust to changes of orientation of adjacent columnals more easily than the thicker columnals of the dististele.

The number of internodals increases away from the cup until a maximum number of columnals in a noditaxis is attained i.e. fourteen columnals, 3424341434243N (Pl. 73, fig. 1). No further internodals are added after this configuration has been attained, and all noditaxes of the dististele have this arrangement of columnals. A theoretically perfect noditaxis would have two further quart-internodals, i.e. 434243414342434N. This is not the case, however, and the reason why this particular internoditaxis configuration is attained remains unknown. The internoditaxis (text-fig. 1b) pattern is symmetrical about the priminternodal, implying that formation of new internodals has occurred evenly throughout the noditaxis. The sequence of columnal insertion is similar (but not identical) to that of the Muschelkalk (middle Triassic) species *Encrinus liliiformis* (text-fig. 5; Linck 1954; Raup and Stanley 1978, p. 48 fig. 3.2) and numerous other examples from the fossil record.

The first cirrinodals occur close to the bottom of the cup, although the nodals closest to the cup are nudinodals; therefore, cirrinodals develop from nudinodals. Columnal calcite is resorbed to form the axial canals (canaliculi) of the cirri which are then formed externally. The cirri are initially extremely short and non-functional as holdfast structures. The first cirri of USNM 12356/1 were composed of two ossicles only. The terminal cirral ossicle is conical and retains the same position throughout growth of the cirrus, becoming claw-like when mature (Pl. 76, fig. 5). The most proximal cirral ossicle
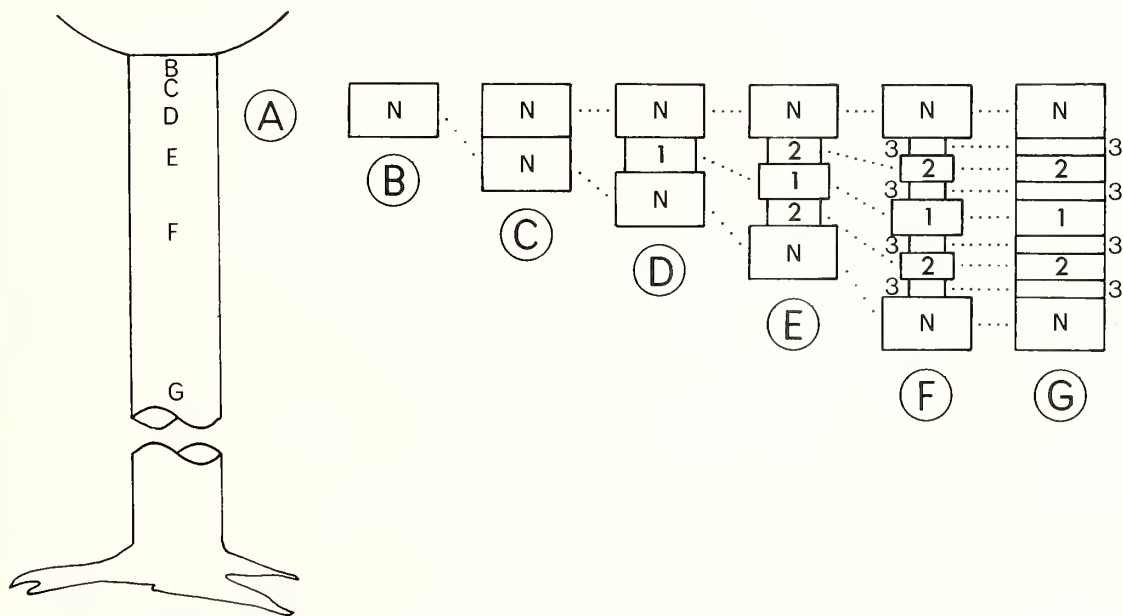

TEXT-FIG. 5. Idealized growth sequence of a heteromorphic stem, based on Raup and Stanley (1978, fig. 3.2) and Linck (1954, fig. 8). A nodal, N (B), is formed beneath the cup. A second nodal is intercalated (C). Prim- (D), secund- (E), and tertinternodals (F) are intercalated between these two nodals (internodal orders labelled 1, 2, and 3, respectively). Further calcite secretion results in all columnals attaining a similar diameter (G). The parts of the stem where stages B–G occur are shown in A.

has a domed proximal facet (Pl. 76, fig. 4) which articulates on the saucer-like cirrus-scar (Pl. 74, fig. 8). The cirri most proximal to the cup do not seem to have this arrangement, but such domed proximal cirral ossicles have developed by the third cirrinodal beneath the cup in USNM 12356/2. If new cirral ossicles are added at the cirrus scar, the domed facet would have to become modified to a planar configuration as each new proximal plate is intercalated. This is unlikely, and it is more probable that new plates are formed between the first two cirral ossicles. These plates are thus of primary importance in cirrus formation, always remaining the most proximal and most distal ossicles, and are here called primary cirrals. The process of cirral ossicle formation is shown diagrammatically in text-fig. 4D–G.

The columnals of the proxistele are initially extremely thin, irregular pentastellate in outline, and lack a crenularium (Pl. 73, fig. 6; text-fig 4C). Columnals grow by increasing in thickness and becoming more regular in outline (Pl. 74, fig. 6). Such columnals are still thin and lack crenulae but show definite tubuli (broad stereom canals arranged around petaloid zones; text-fig. 3). Columnals become apparent externally only when a crenularium is developed, i.e. when the columnals are seen to articulate with adjacent ossicles. This is associated with a further thickening of the columnal and an alteration in outline from pentastellate to petaloid pentagonal (Pl. 74, fig. 1). The ossicle now shows all features of the mature, symplexial articular facet (text-fig. 6B) of all columnals of the dististele (some distal articula have a secondary synostosial articulation, described below) (Pl. 74, fig. 2; text-fig. 3). This final stage of development is attained by further increasing the height and diameter of columnals, increasing the number and amplitude of the crenulae, and reducing the facet concavity of the early formed columnals.

The change from proxistele to dististele occurs after the last noditaxis in which adjacent columnals share five intercolumnal fossulae (Franzén-Bengston 1983). The fossulae of C. decorus are radially orientated, tubular passageways which lie at 72° to each other and are seen as grooves on the articular facet (Pl. 74, fig. 1), i.e. the grooves of adjacent articula combine to produce a tube. The positions of fossulae in the dististele are represented by the axial grooves. The last proximal columnal of USNM 12356/2 is the most distal nodal of the sequence described above (text-fig. 4H). It is also the first nodal to show a good synostosial articulation (i.e. facets are smooth; text-fig. 6A) with the next distal internodal.
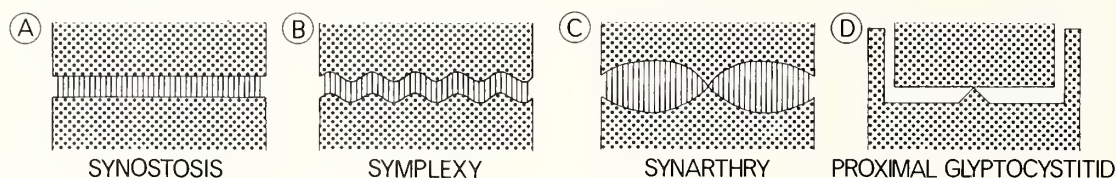

TEXT-FIG. 6. Articulations between columnals (ligaments shown as vertical rulings in A–C). A, a synostosis; adjacent facets are planar. B, a symplexy; two interlocking crenularia (text-fig. 3) composed of ridges (culmina) and grooves (crenellae). C, a synarthry; opposed faces rock on adjacent ridges. D, proximal glyptocystitid; a 'see-saw', in which a planar facet rocks on a fulcral ridge. (A–C, after Lewis 1980; D, after Paul 1968).

EXPLANATION OF PLATE 74

Figs. 1–10. *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson). USNM 12356/1. Scanning electron micrographs of columnals. 1, 6, 7, columnals from the proxistele: 1, articular facet, × 12; 6, articular facet of a cryptic internodal, × 12; 7, oblique view of a nodal facet showing the dish made by the interrays (note broad meshwork of lateral stereom which extends into the fossulae), × 25. 2, proximal facet of a nodal of the dististele, × 12. 3, 4, synostoses of the dististele: 3, stereom growth into the lumen of a nodal, × 200; 4, nodal facet, × 12. 5, 8, cirrus scars: 5, the left-hand scar encroaches on to the adjacent infranodal, the other being limited to the nodal, × 15; 8, cirrus scar, showing the elliptical lumen and the synarthrial ridges, × 50. 9, 10, stereom of the symplexial facet: 9, petaloid zone, × 50; 10, interpetaloid zone (note tubuli), × 50.

PLATE 74

DONOVAN, *Chladocrinus* (*Neocrinus*)
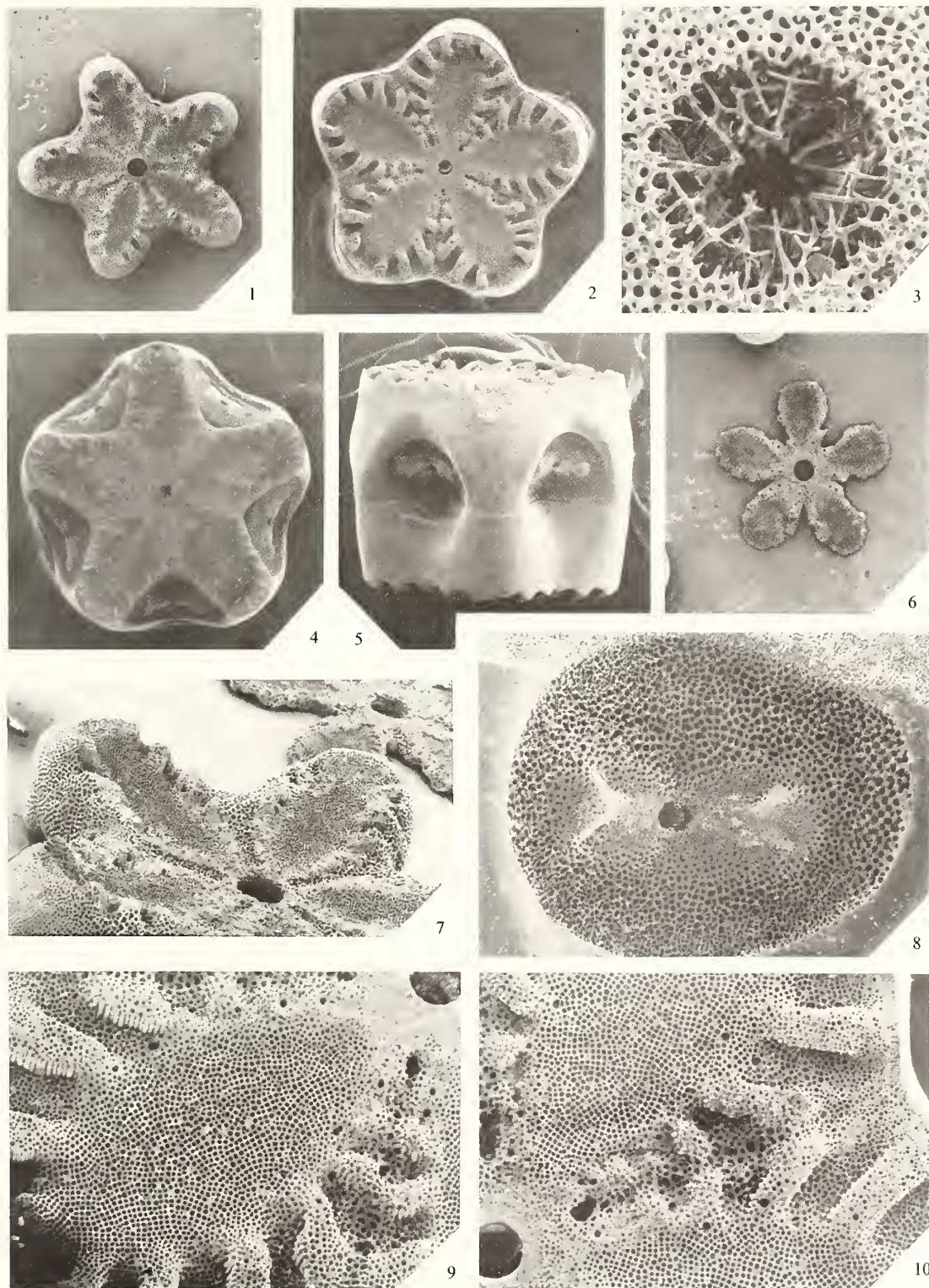
The dististele is composed of noditaxes of a constant configuration i.e. 3424341434243N (Pl. 73, fig. 1). All internodals are pentagonal in outline, with well-rounded angles and sides infolded to give a flower-like appearance to the facet. Latera of internodals are gently convex. A reducing sequence of columnal heights from priminternodals to quartinternodals distinguishes the various internodal orders. The nodals are taller than the internodals, with latera that are more convex. Nodals are thus the widest columnals of the dististele. Nodals are further distinguished by having five distally orientated cirrus scars in radial positions on the lower half of the latus, i.e. they are cirrinodals (text-fig. 1c).

Almost all articula of the dististele resemble those of Pl. 74, fig. 2 and text-fig. 3. The only exceptions are the distal facets of nodals and the proximal facets of adjacent internodals, which have a synostosial articulation. The terminology used in text-fig. 3 follows Roux (1977b, p. 46) and Moore et al. (1968), except that the term 'large meshes' is replaced by tubuli (singular, tubulus; see explanation above). The petaloid zones are interradial.

The configuration of the facets of my specimens does not agree completely with Roux's diagram of the same area (1977b, fig. 19); they have rectilinear stereom (Smith 1980) with diamond-shaped meshes in the five areola pits (Pl. 75, fig. 7). This is indicative of strong ligamentation in these areas. In transverse section the areas of rectilinear stereom of the columnal appear oval to pear-shaped in outline (text-fig. 4A). The areolar pits also have pear-like outlines. Nine to twelve crenulae border each petaloid zone. The tubuli form an irregular border around the areola petals but do not reach the margins of the columnal. The crenularium can be open or closed and an interpetaloid axial groove separates each pair of crenularia (Pl. 74, figs. 9, 10). Pl. 74, fig. 2 and text-fig. 3 show only areolae with open crenularia, but this is not always the case (Pl. 74, fig. 9; Roux 1977b, fig. 5c). Roux did not mention the possibility of open crenularia when discussing this species.

The distal articulum of each nodal, and the proximal facet of the sequential, distal tertinternodal (called the infranodal by Breimer 1978, p. T24), have synostosial articulation facets (Pl. 73, figs. 1, 3, 5; Pl. 74, figs. 4, 5). These are secondarily modified from symplexial articulations (compare text-fig. 6A and B) by infilling with stereom (Roux 1974, p. 6) and have been called cryptosymplexies by some authors (e.g. Moore et al. 1968). Relict crenulae are apparent at the edge of some synostosial articula (Pl. 73, figs. 3, 5). It is almost impossible to break (mechanically) a column along such a stem joint; the stem will normally break through a symplexial suture, or partly through both suture and plate. Synostosial joints therefore have extremely strong ligamentation. Such stem joints, however, are thought to be adapted for autotomy, i.e. self-mutilation as a defence mechanism (Emson and Wilkie 1980).

Lumina (singular, lumen: the intersection between the axial canal of the column and an articular facet) show little variation in shape or diameter along the whole column. The lumen at the base of the cup is pentagonal with rounded angles (Pl. 73, figs. 2, 7). This pentagonal outline is retained by columnals in the most proximal part of the stem (Pl. 73, fig. 6; text-fig. 4c) but most plates have circular lumina. For example, in USNM 12356/1 the most distal columnal with a pentagonal lumen is the second priminternodal beneath the cup. The transition from pentagonal to circular is gradual, not sudden.


EXPLANATION OF PLATE 75

Figs. 1–9. *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson). USNM 12356/1. Scanning electron micrographs of stereom microstructure. 1, 2, 4, 8, longitudinal section through a pluricolumnal of three internodals from the dististele: 1, rectilinear (centre) and labyrinthic stereom, the latter concentrated in the interpetaloid zones, ×30; 2, rectilinear stereom adjacent to the axial canal (right), ×100; 4, sequence of columnals (taxis) in section, ×15; 8, section through a petaloid zone, showing the interlocking crenulae, ×60. 3, rectilinear stereom of a crenula, ×60. 5, interpetaloid zone of a synostosis, showing tubuli, ×55. 6, stereom infilling axial canal at distal end of the most distal columnal, ×100. 7, rectilinear stereom of a petaloid zone, ×400. 9, stereom at the edge of a columnal, ×550.

PLATE 75

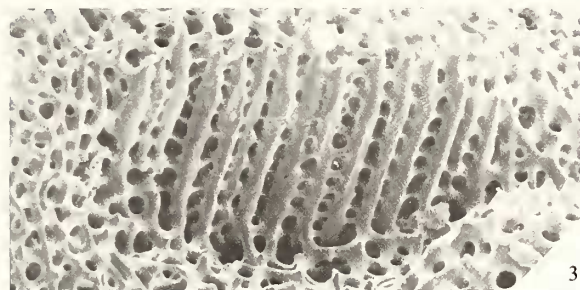DONOVAN, *Chladocrinus* (*Neocrinus*)
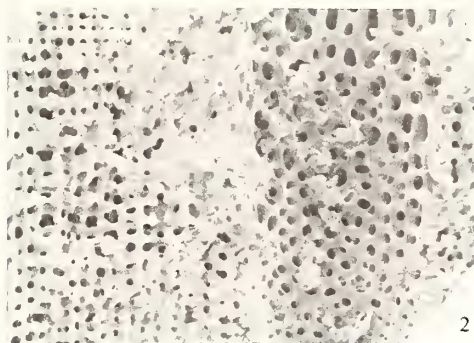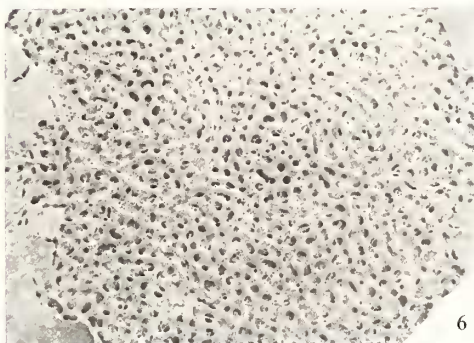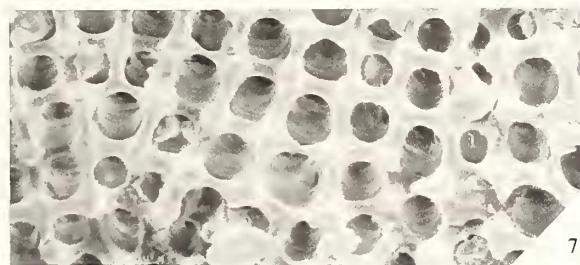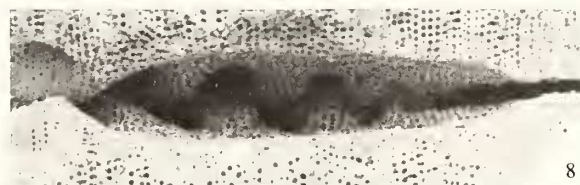
The shape of the lumen is modified in two areas of the dististele. The lumina of synostoses are partially infilled by long, spike-like, labyrinthic stereom fingers which grow into the axial canal (Pl. 74, fig. 3; Roux 1977b, fig. 8). This must limit the amount of soft tissue in the axial canal adjacent to synostoses (cf. Pl. 74, fig. 3 and Pl. 75, fig. 2). Such an ingrowth of stereom suggests that the axial canal can be infilled rapidly by calcite growth if autotomy occurs at a synostosial stem joint. The axial canal of the synostosial facet of the most distal columnal is completely filled by labyrinthic stereom (Pl. 75, fig. 6) and no suggestion of the outline of the lumen is preserved. In all other respects this columnal resembles the distal facet of any nodal of the dististele (e.g. Pl. 74, fig. 4). The axial canal is also modified in the regions within nodals in which the lateral extensions into the cirri arise (canaliculi; text-figs. 1, 4). In these regions the axial canal is pentagonal in outline, becoming pentastellate at the junction with the cirral canals.

Cirri are attached to the column at the five cirrus scars which are present on each nodal (Pl. 73, fig. 1; Pl. 74, figs. 5, 8). These occur on the distal part of the latus and are orientated so that cirri always point away from the cup (Pl. 74, fig. 5; text-fig. 2; Breimer 1978, p. T24, fig. 11). Cirrus scars may be limited to the nodal or they may overlap on to the adjacent infranodal (Pl. 73, fig. 1; Pl. 74, fig. 5). They are elliptical in outline with a central, elliptical axial canal which is flanked by a pair of synarthrial articular ridges (Pl. 74, fig. 8). The ectoderm covering the column is probably continuous over the cirri.

The cirri of the proxistele have been discussed above. Cirri and cirral ossicles of the dististele are illustrated in Plate 76. An entire cirrus is approximately 17 mm long and is composed of twenty-six cirrals (Pl. 76, fig. 1). The most proximal and distal cirral ossicles (Pl. 76, figs. 4, 5, respectively) are the two primary cirrals, which were defined above. The proximal primary cirral has a domed proximal facet which fits the cirrus scar. The lumen is approximately elliptical (Pl. 76, fig. 3) but the axial canal of the cirral ossicle has two central ridges on the long sides which gives the appearance of a figure '8' to the aperture. The lumen is flanked on the articulum by two notches which articulate against the ridges of the cirrus scar. This differs from columnals with synarthrial ridges (text-fig. 6C), such as platycrinitids (Moore 1939b) and Ristnacrinus (Chauvel and Le Menn 1972), in which the articulation is formed by two opposed ridges. It is, perhaps, more analogous with the 'see-saw' articulation of the glyptocystitid cystoids (text-fig. 6D; Paul 1968). The arrangement of ridge and groove is presumably more resistant (than two ridges) to a force acting to twist the cirral ossicle against the cirrus scar, e.g. eddy currents. The distal facet is approximately planar, with a slightly raised margin of stereom, so that the next distal cirral ossicle fits into it like a cup on to a saucer (Pl. 76, fig. 6). Similar articulation is shown by all cirral ossicles, except the distal primary cirral.

The proximal cirral ossicles are low but cirral height increases distally until they become slightly higher than wide (Pl. 76, fig. 1). The most distal cirral ossicles taper and are reduced in height, terminating in the claw-like, distal primary cirral (Pl. 76, figs. 1, 2, 5), i.e. cirral height is a maximum in the centre of the cirrus. The lumen becomes excentric in the middle cirrus (Pl. 76, fig. 7). The articulation surfaces are dorsal to the axial canal in this area, so that the cirrus has a preferred distal flexure. This effect is further aided by the articular facets being angled to the latera (Pl. 76, fig. 1). This excentricity and the nature of the stereom around the axial canal suggest unequal development of

EXPLANATION OF PLATE 76

Figs. 1–8. *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson). USNM 12356/2. Scanning electron micrographs of cirri. 1, complete, mature cirrus (proximal end at the bottom of the photograph), × 8. 2, 5, 8, distal, claw-like primary cirral: 2, articular facet, × 120; 5, latus, × 55; 8, stereom microstructure of the latus, × 200. 3, 4, proximal facet of the most proximal cirral: 3, lumen, × 400; 4, oblique view of curved articular facet, slightly damaged to expose the internal stereom, × 55. 6, articulation between sequential cirrals, × 55. 7, facet of a cirral from the central part of the cirrus (note the excentric axial canal), × 55.
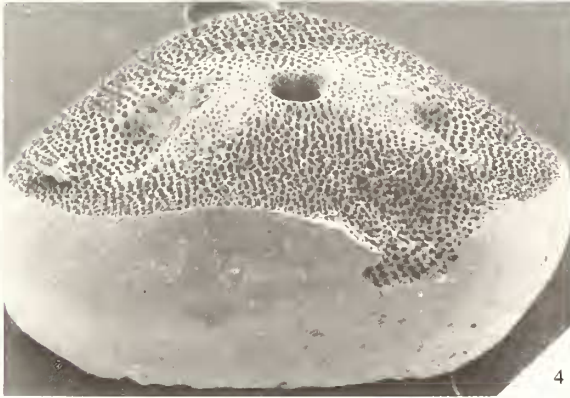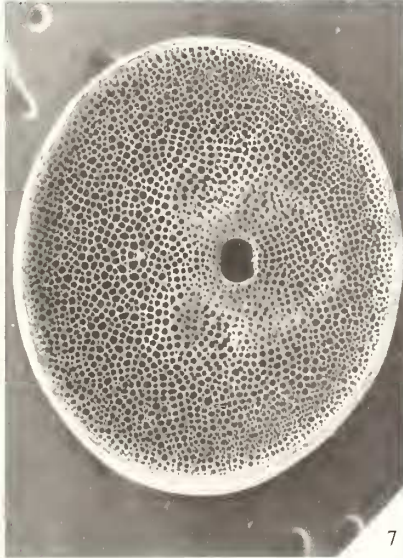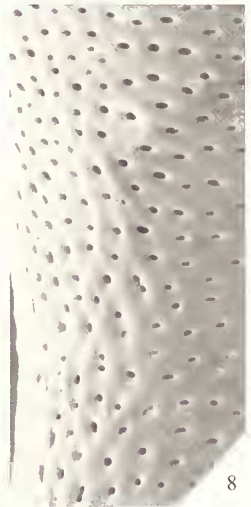
PLATE 76

DONOVAN, *Chladocrinus* (*Neocrinus*)
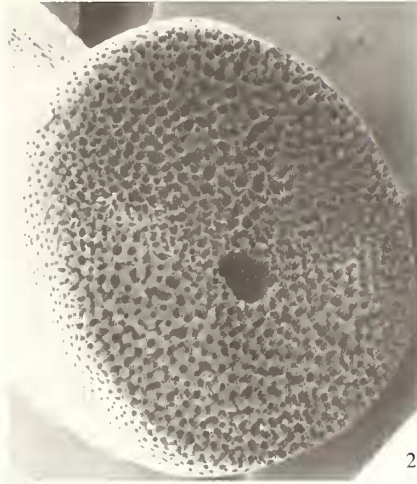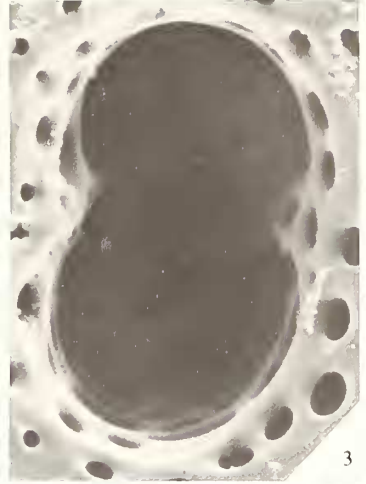
a contractile apparatus and a preferred flexure away from the cup, as in comatulids (Holland and Grimmer 1981). The distal primary cirral has an articular facet which is angled in the area of synarthrial articulation (Pl. 76, figs. 2, 5). The lumen is elliptical, excentric, and situated on the axis of articulation.

The five axial canals of the cirri are connected to the main axial canal of the column by curved canaliculi in the nodals (text-fig. 4A, B). The canaliculi are curved in the same direction as the preferred curvature of the cirri. It is possible that a swollen termination of nervous tissue exists in the zone where the cirral axial canals diverge. In the event of autotomy and loss of the stem distal to any nodal of the distal stem, the rapid growth of stereom is assumed to infill the axial canal up to the base of this termination.

STEREOM MICROSTRUCTURE

Stereom microstructure was examined on cleaned ossicles (Pl. 75; the columnal illustrated in Pl. 73, fig. 4 shows the concentration of ligament fibres in the petaloid zones). The stereom of the petaloid zones (Pl. 74, figs. 9, 10; Pl. 75, figs. 3, 7, 8), cirrus scars (Pl. 74, fig. 8) and cirral facets (Pl. 76, figs. 2, 4, 7) is of the type called α-stereom by Roux (1970, 1975, 1977b). Smith (1980), in his revision of stereom microstructure, recognized two types of α-stereom: rectilinear and galleried. The stereom of the petaloid zones (Pl. 75, fig. 7) is rectilinear, although that of the culmina (Pl. 75, fig. 3) is apparently galleried. Latera (Pl. 75, fig. 9; Pl. 76, fig. 8) appear to be composed of the simple perforate stereom of Smith. The stereom of the interpetaloid zones (Pl. 74, fig. 10) is labyrinthic (= β-stereom of Roux). Longitudinal sections of pluricolumnals show that rectilinear stereom is concentrated in the region of the axial canal and of the petals (Pl. 75, figs. 1, 2, 4), while other regions are composed of labyrinthic stereom. Sectioning has also revealed the close contact between articulating crenulae (Pl. 75, fig. 8). The stereom of the synostosial articula (Pl. 74, fig. 4; Pl. 75, fig. 5) is a labyrinthic layer (synostosial stereom of Roux 1977b, p. 47) which has overgrown a normal symplexy. Tubuli are present on these articula, in similar positions to those of the symplexial articula. It is probable that these canals penetrate the entire column.

BIVARIATE ANALYSIS OF COLUMNALS

Only three features discussed in previous columnal studies are considered in this section: columnal diameter (KD), columnal height (KH), and lumen diameter (LD). Features such as the length/breadth ratio of the petaloid zone show little variation, and the number of culmina varies in an irregular manner even between petals of a single articular facet (text-fig. 3; Roux 1977b, p. 62, fig. 19). In an attempt to generate an artificial 'palaeontological' sample, the KD/LD and KD/KH graphs (text-fig. 7A and B, respectively) are based on a random sample of columnals from the proxistele of USNM 12356/1 and the disisteles of both specimens. These graphs are somewhat artificial because the forty-one plotted points are based on information derived from only two individuals, whereas a similar collection of fossil columnals could come from forty-one individuals. The KD/LD plot (text-fig. 7A) shows that lumen diameter remains almost constant as columnal diameter increases, although there is a slight decrease in lumen diameter with columnal growth. This differs from many examples from the fossil record, in which lumen diameter increases with increased columnal diameter. The KD/KH plot (text-fig. 7B) gives a good linear grouping of columnals apart from one narrow, low columnal, an internodal from the proxistele. Such comparatively thin columnals are less likely to be preserved than the more robust, and plentiful, ossicles of the disistele. Lines of best fit have been calculated using the Bartlett method (Fryer 1966).

It is not intended to discuss here the functional morphology of the isocrinid column, which is summarized in Rasmussen (1977). Similarly, ecology of modern stalked crinoids is discussed by Macurda and Meyer (1974, 1983). Soft tissues of these specimens has deteriorated over the past hundred years and has not been studied in detail. The anatomy of modern crinoids has been reviewed by Breimer (1978).
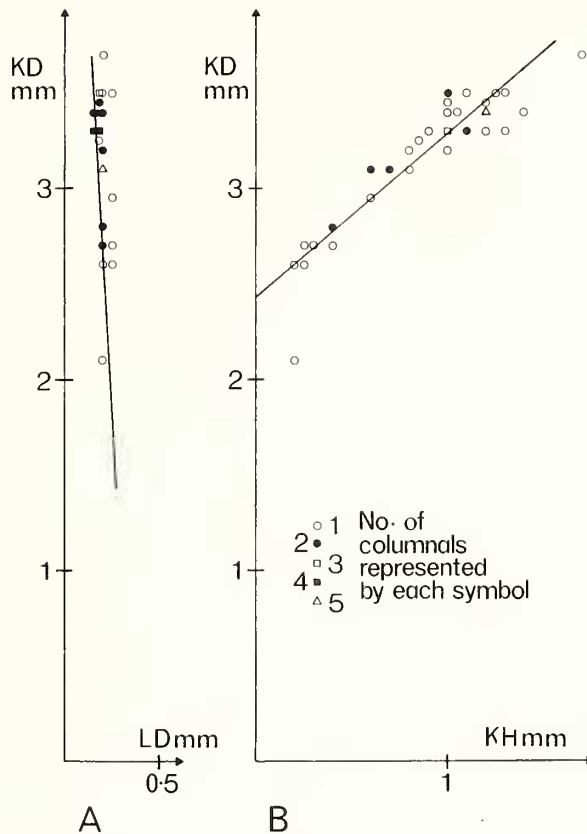
TEXT-FIG. 7. KD/LD (A) and KD/KH (B) graphs for *Chladocrinus*
(*Neocrinus*) *decorus*. KD, columnal diameter; LD, lumen diameter;
KH, columnal height.

CONCLUSIONS

From the above survey of the column morphology of *C. decorus*, the following comments are made which may prove to be of general significance in all crinoids.

1. The diameter and shape in cross section of the axial canal is almost constant along the whole length of the stem. The only columnals which do not have a circular lumen are those of the most proximal part of the column and the distal facets of cirrinodals. This arrangement agrees with the intuitive conclusion that adjacent columnals must have lumina of similar morphology. It would not be expected that, say, a columnal with a pentastellate lumen would articulate with a columnal in which the lumen is circular. The shape of the axial canal, however, is not necessarily the same as that of the column.

2. Columnals change shape during growth, although their arrangement in the stem (of this example, at least) is regular. Adjacent articula always have similar morphologies, e.g. symplexial and synostosial articula are never in direct contact with each other. This is true in both columnals and cirrals. Cirral facets are not necessarily the same as those of columnals from the same stem.

3. Noditaxes become regular and fixed in their arrangement of columnals, particularly away from the main growing area. Only nodals bear cirri. Only nodals and infranodals have different articula on the same columnal, i.e. both have a symplexy on one articulum and a synostosis on the other.

4. Cirrus morphology is usually quite different from that of the associated column. Cirrus growth is different from that of crinoid arms (in which new ossicles are added at their tips) and columns, with new cirral ossicles being intercalated just distal to the most proximal primary cirrus.

5. Some columnals from the growing region (proxistele) are too small to be seen externally and can only be detected when the column is disarticulated or sectioned. Information about them will be lost in fossil pluricolumnals which are preserved as external moulds.

6. Some fine details which can be seen in *C. decorus* may be too delicate to be fossilized, e.g. the stereom infills of some axial canals (Pl. 74, fig. 3). However, good stereom is known to be preserved in some of the earliest echinoderm fossils (Donovan and Paul 1982).

The observation that axial canal outline is less variable than the columnal shape is important when assessing the relative merits of the two existing systems for naming dissociated crinoid columnals. That of Moore (1939a; Wright 1983) is based on both columnal and lumen outline, the name which is generated describing these features, e.g. a columnal with a pentagonal outline and a circular lumen would be placed in the morphogenus *Pentagonocyclopa*. In this system the first part of the generic name describes the columnal outline, which is presumably regarded as being more important than the lumen outline. The method of columnal naming used by Russian authors (Yeltysheva 1955, 1956) is similar, but the lumen outline is regarded as being the more important of the two parameters, e.g. the above columnal would be placed in the morphogenus *Cyclopentagonalis*. The stem morphology of *C. decorus* suggests that the latter system is to be preferred. The lumen outline and facet articulation are more important than columnal shape in columnal classification, and for reconstruction of stems from dissociated ossicles.

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S. K. DONOVAN

Jane Herdman Laboratories of Geology
University of Liverpool
P.O. Box 147
Liverpool L69 3BX

Present address

Department of Geology,
Trinity College,
Dublin 2, Eire